NEMATODES AND THEIR RELATIONSHIPS.[1]

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INTRODUCTION.

THE soils of our yards, gardens, and fields swarm with thousands of kinds of minute animals and plants of which we know little or nothing. We depend on the soil for our very existence, and it may seem that this fact should have caused us long ago to make ourselves thoroughly acquainted with it and all its inhabitants; yet the truth is otherwise. Here beneath our very feet are microbes, protozoa, fungi, and many other kinds of small organisms, thousands of species, of which we know hardly the first thing beyond the mere fact of their existence. In some ways this ignorance extends even to the higher plants and animals. Confront the ordinary botanist with the complete root system of one of our common plants and ask him what it is and the chances are he will have to confess his ignorance. While his knowledge of the above-ground parts of the higher plants is most systematic and extensive, in most cases the corresponding parts below the surface of the ground are almost wholly unknown to him.

Relatively speaking, then, in a biological sense, this soil we daily tread under foot is almost a veritable terra incognita. Why is this so? It is difficult to formulate a reasonable answer. The fact is that our biological researches as a rule do not extend below the surface of the ground. This lamentable fact is, of course, an answer to the question, but it does not seem a reasonable one.

Inhabiting the soil in myriads, hidden behind this veil of ignorance, there is a group of organisms known as nematodes. Some members of this group have forced themselves on our attention by the enormous damage they do to crops. These, however, so far as numbers are concerned, constitute a very

[1] The illustrations are mostly from drawings made from nature under the author's direction by Mr. W. E. Chambers. Figures 1 and 19 are from the author's drawings, and figure 10 was prepared by Miss Ella Welborn from the basis of Schepotieff's plates.

insignificant minority. There are multitudes of others, some only in a lesser degree injurious, still others that are beneficial, and yet others, the great majority, of unknown

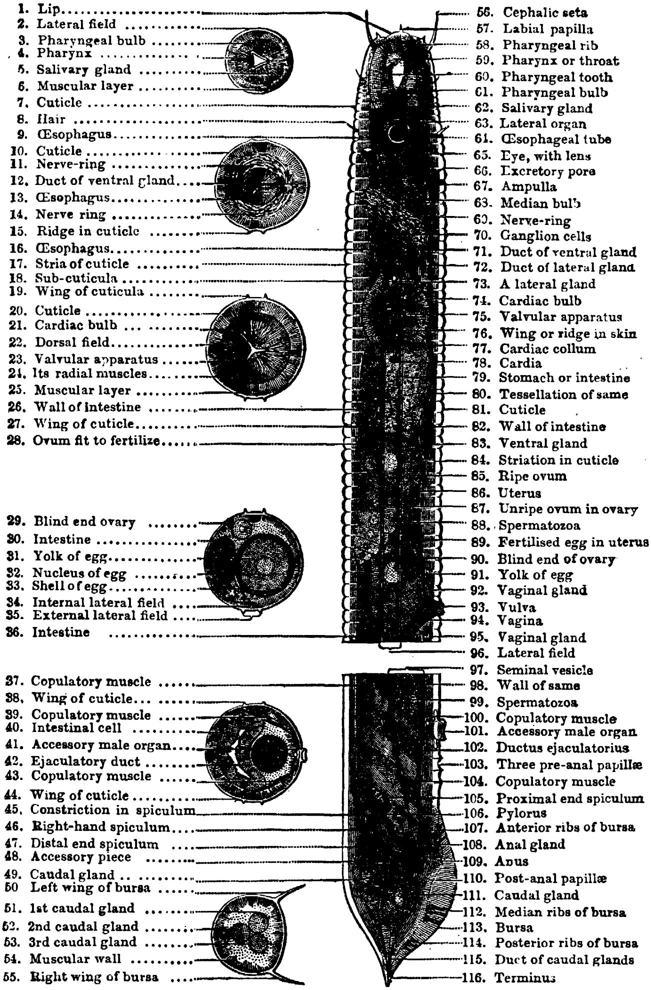

FIG. 26.—Diagrammatic representation of the nematode anatomy. The upper part of the figure and four corresponding circular cross sections at the left represent the anterior half of a female nematode seen from the right-hand side. The lower part of the figure and the two corresponding cross sections represent the same view of the posterior part of a male nematode. The cross sections are placed opposite the portions of the side view to which they relate.

economic significance. So little do we know of this vast multitude of soil-inhabiting nematodes that the first spadeful of earth we lift is practically certain to contain kinds never seen before (fig. 27). Numerous as are the nematodes inhabiting the soil, the aquatic species are even more numerous. Furthermore, thousands of species of nematodes occur as parasites in animals and plants.

At present our knowledge of this group, such as it is, is confined to a comparatively small number of people. The reasons for this are not far to seek. If we consider any group of animals the study of which is popular—as, for instance, birds—we find the individuals of that group both large and numerous, and, moreover, much in evidence; and it will be found, in most cases, that they are serviceable to man; they furnish him food, raiment, or some other valuable material; or they are ornamental,

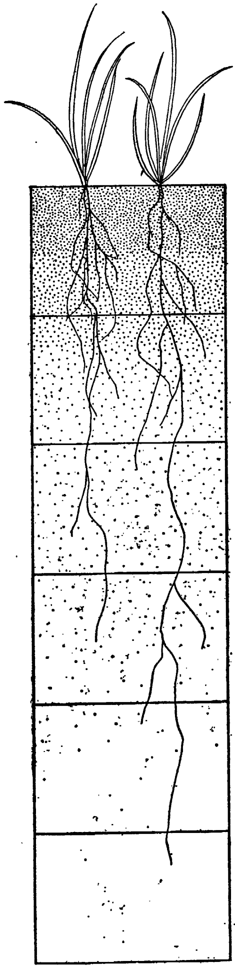

FIG. 27.—Diagram representing the upper foot of soil, and showing the relative abundance of nematodes in each successive 2 inches. Derived from a low-lying alluvial soil carrying about 3,000,000,000 nematodes to the acre. Most of the nematodes are in the upper 3 inches. Though shown distributed uniformly in each layer, they are really most numerous about the roots of plants.

or attractive as pets, or useful in some other way. Now, it is not unfortunate for the nematodes that they are none of these, but it is unfortunate for us, if on that account we are prevented from knowing much that would be most useful to us, as well as interesting and diverting.

Nematodes do not furnish hides, horns, tallow, or wool. They are not fit for food, nor do they produce anything fit to eat; neither do they sing or amuse us in any way; nor are they ornamental—in fact, when they are displayed in museums the public votes them hideous. Lacking in all these respects, they fail even in furnishing any moral or praiseworthy example; they are not known to be industrious like the ant, or provident like the bee, indomitable like the spider, or frugal, or honest, or anything else that is admirable. What claim, then, one may ask, can such beings lay to our attention? I think I hear some outraged naturalist exclaiming in reply: "And must a thing be useful to deserve attention? Must a thing have an assessed money value to be worthy of study? Is there no idea above meat for dinner and raiment for the reception? Is everything to be measured by its value in dollars and cents? Thank God, there are some things so far removed from the lucre system we allow to dominate our lives that it is as impossible to measure the one in terms of the other as it would be to buy a ticket into Heaven." I should have a good deal of sympathy with the man whose wrath boiled over in this manner and found expression in such burning language, but, at the same time, I confess I should have more hope of converting others to my way of thinking by adopting another tone and different tactics. Descending to one of the lowest planes on which an appeal could be made, I should say that, if, for example, it could be proved that nematodes would draw as a show to such an extent as to cause the populace to part with half a dollar each for a place in the balcony, a dollar or two for the dress circle, and all the rest of it, we might feel their claims for attention to be meeting with some little encouragement. Such a demonstration would be more forcible than any tirade against even the most reprehensible prejudice.

But it is unnecessary to descend to any such appeals to show the advisability of more fully acquainting ourselves with these organisms, for although, so far as we know at present, nematodes may not often be directly beneficial to man, a knowledge of them would be useful to every person, simply because, though he may not know it, he is infested by them, either continually or from time to time. This unpalatable fact needs no proof to the initiated; but those not informed will doubtless be surprised to learn that no less than about 50 kinds of nematodes are known to infest the human body.

Our domesticated animals suffer in like manner, and even more severely (fig. 28). Thus, in countries where the wealth consists largely in live stock, as, for instance, in the western part of this country, in Australia, and in the Argentine Republic, the monetary loss caused by nematodes is always considerable, and sometimes very great. The parasitic nematodes shown on this page exist in millions in most of the great sheep-growing countries; these are only a fraction of the species of nematodes that attack sheep, and are mentioned simply as embodying a typical case among our domesticated animals. To every person, therefore, and especially to medical men and veterinarians, these parasitic nematodes should possess no common interest.

FIG. 28.—Natural-size figures of some of the nematode parasites of the sheep: *a*, *b*, Found in the duodenum; *c*, in the intestine; *d*, in the stomach, very common and injurious; *e*, in the intestine, very common and injurious; *f*, in the anterior part of the small intestine, inflicting severe bites; *g*, in the large intestine. These are only a fraction of the nematodes known to infest the sheep.

Nor are the crops of the farmer free from the attacks of these creatures. Wheat, the sugar beet, coffee, and scores of other crops are frequently decimated or even ruined by diseases caused by the attacks of microscopic nematodes.

Beyond doubt a complete knowledge of nematodes, if properly applied, would enable us to save a vast amount of life and treasure and prevent a vast amount of suffering.

But it is by no means entirely for these reasons that I would like to see these organisms receive a greater amount of attention. They possess a powerful interest because of the unusually clear view they give us of the various processes relating to life, and I believe this fact could easily be turned to educational account; in fact, I know it could. In the contemplation and discussion of one of these organisms, I have seen the statesman forget his social problems, the judge his law, the mathematician his quantities, the artist his art, the philanthropist his schemes, and exclaim and question in terms of enthusiasm and interest concerning which there could be no doubt.

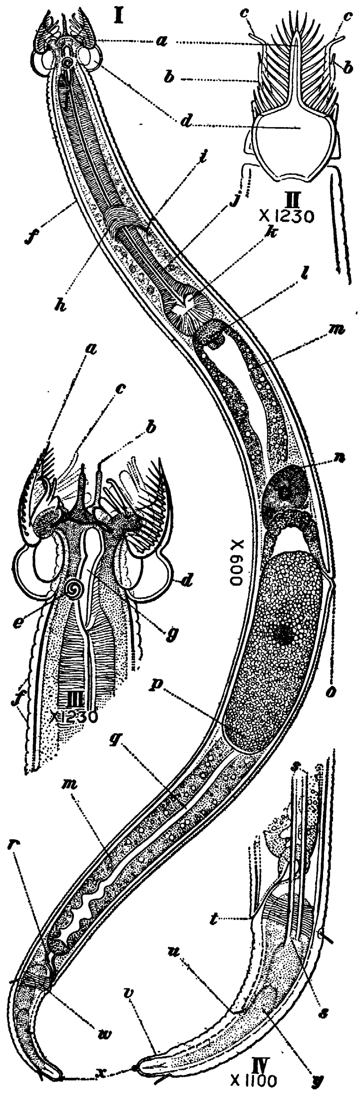

FIG. 29.—A very remarkable nematode, Wilsonema, found in soils in various parts of the United States. How it can make its way through the soil without damage to its wonderfully complicated and delicate mouth parts is a mystery. *I.* Lateral view of female; *II,* dorso-ventral view of the head of the same individual; *III,* enlarged lateral view of the head of same individual; *IV,* lateral view of the tail end. *a,* Ventral appendage, which, together with the corresponding dorsal appendage, acts as a sieve; *b,* lateral tactile organ associated with the sifting apparatus; *c,* internal elements (supports?) of the sieves; *d,* inflated valvular apparatus; *e,* amphid; *f,* cuticle; *g,* pharynx; *h,* nerve ring; *i,* excretory pore; *j,* esophagus; *k,* threefold valve of the cardiac bulb; *l,* cardia; *m,* wall of intestine; *n,* flexure of anterior ovary; *o,* vulva; *p,* egg; *q,* lumen of intestine; *r,* rectum; *s,* lateral wings; *t,* anus; *u,* caudal seta; *v,* spinneret; *w,* anal muscles; *x,* apical portion of spinneret; *y,* one of the three caudal glands.

Formerly it was my duty, as professor of biology, to bring before the students in my courses, first in a secondary school and later in the university, a series of animals and plants for dissection and study, and I can safely say that no organisms excited so much interest among those young men, or furnished them with a greater amount of instruction, than small species of free-living nematodes. These little animals present a wonderful complexity of organization combined with such transparency that very little is hidden from view. Digestive system, nervous system, excretory system (fig. 29), muscular system, sexual system, all are to be seen with most instructive wealth of detail and in full action in the living animal. My experience in this matter makes me very confident in saying that professors of biology could do far worse than to introduce into their courses a more careful examination of these creatures.

FIG. 30.—The asymmetrical nematode, Bunonema. This apparently deformed little creature presents relatively monstrous warts on one side of its body. It belongs to a large group, usually to be found in decaying matter.

NEMATODES AND THE NEW SCIENCE OF HEREDITY.

If it were necessary to fortify these assertions, I might call attention to the fact that since the days of Leeuwenhoek and the invention of the microscope these organisms have excited a keen interest in the minds of great naturalists. Anyone will be convinced of this by even a casual glance at the literature relating to any one of several common species—for instance, the nematode so common in table vinegar and popularly known as the "vinegar eel." I might also call attention to the fact that some of the most momentous of all our scientific discoveries have been made through the instrumentality of nematodes; witness the discovery of the formation of the polar bodies in the ovum, the coalescence of the spermatic nucleus with that of the ripe ovum, and the subsequent cell-division phenomena, leading up to a science of heredity. The clarity of the nematode egg makes it particularly suitable for investigations of this kind.

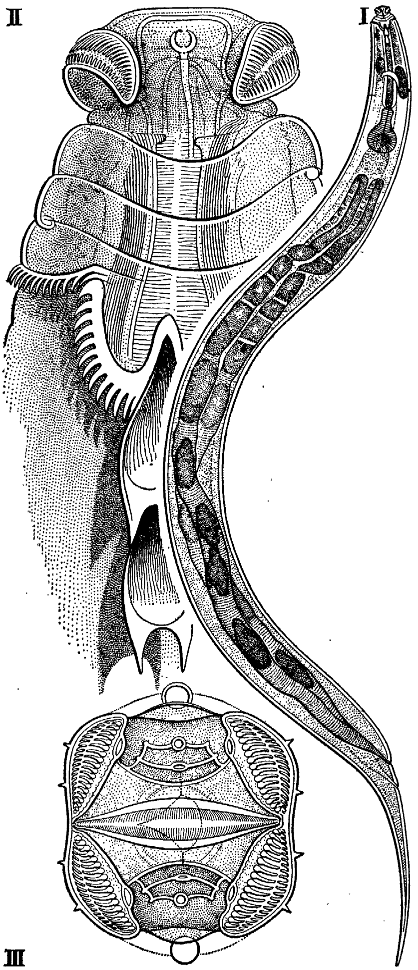

FIG. 31.—A remarkable nematode, called Heth, notable on account of the numerous sieves through which it sifts its food, and also on account of the acute backward-pointing barbs, of relatively large size, with which its head is armed.

If one removes from the small part of one of the ovaries of the common lung worm of the frog, *Rhabdias nigrovenosa,* an egg that has not yet begun to segment, and places it in water under a microscope magnifying 300 to 400 diameters, he may easily observe one of the most impressive and instructive of all the phenomena of life—the formation of a young animal inside the egg. This egg, which is at first a single cell, becomes in the course of a few hours under our very eyes a living, actively moving animal. This impressive spectacle begins by the formation from the original cell of two others of slightly unequal size, the change being accompanied by the karyokinetic phenomena concerning which there is nowadays so much discussion and research. Each of these cells again divides, and so the rhythmic change goes on, giving rise to tissue after tissue and organ after organ, until the baby nematode lies before us complete and ready to begin its active battle for existence. The observer rises at last, feeling that he has indeed approached as near to the mystery of life as it is yet given to man to approach.

We are gradually rebuilding the science of heredity, and one of the basic facts of this renovation is the union of the nuclear material of two parent cells to form the nucleus from which the offspring grows. This flow or transportation of nuclear material from parent to offspring is a matter of supreme interest and is now being studied with the minutest care, and is found to follow laws capable of such exact definition that we are able to base upon them predictions as to the nature of the offspring. Practical results of vast importance in the breeding of animals and plants are, therefore, now only a matter of time.

The fundamental facts in this very important new science came to light through observations upon the eggs of nematodes. It was in a nematode egg that it was first observed that the animal male and female nuclei actually coalesce to produce the new compound nucleus, or pronucleus, which alone is capable under the usual normal conditions of growing and producing a new individual.

Again, it was in the nematode egg that it was first proved that the pronucleus when it divides sends into each of the two new cells a definite portion of the matter it derived from each parent. Both of these discoveries are absolutely fundamental and of enormous practical significance.

It is no wonder, therefore, that there should exist on the part of those most familiar with these fields of research, a wish that our knowledge of nematodes should be increased and brought to the attention of a larger number of people.

An old adage assures us there is no royal road to knowledge. There is certainly no royal road to a knowledge of nematodes. The traffic in this direction has not justified the installation of through trains and sleeping cars; so he who takes this route must be prepared to put up with inconveniences, and to make the best of certain disgusting passages. To the squeamish, the lazy, the impatient, the inaccurate, about to take tickets for this journey, I should say, "Don't do it! It won't suit you." But to him not afraid of work, brave under discouragements, patient, cautious, and with a good

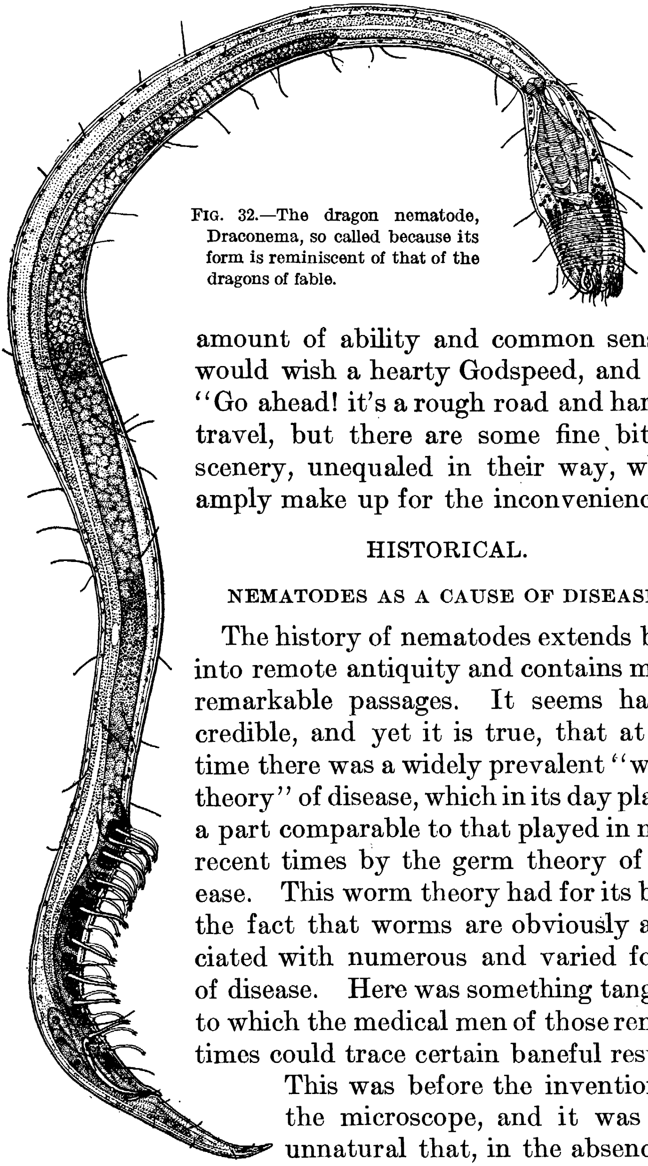

FIG. 32.—The dragon nematode, Draconema, so called because its form is reminiscent of that of the dragons of fable.

amount of ability and common sense, I would wish a hearty Godspeed, and say, "Go ahead! it's a rough road and hard to travel, but there are some fine bits of scenery, unequaled in their way, which amply make up for the inconveniences."

HISTORICAL.

NEMATODES AS A CAUSE OF DISEASE.

The history of nematodes extends back into remote antiquity and contains many remarkable passages. It seems hardly credible, and yet it is true, that at one time there was a widely prevalent "worm theory" of disease, which in its day played a part comparable to that played in more recent times by the germ theory of disease. This worm theory had for its basis the fact that worms are obviously associated with numerous and varied forms of disease. Here was something tangible to which the medical men of those remote times could trace certain baneful results. This was before the invention of the microscope, and it was not unnatural that, in the absence of microscopes to reveal the enormous prevalence of micro-organisms, there should spring up and become widely accepted a theory that worms were a general cause of disease, and that even those diseases not obviously due to this cause were in reality due to it through some means not yet understood. Of all the organisms that inhabit the human body none are more prominent or more likely to come under the observation of the physician than certain of our nematode parasites—indeed a knowledge of these nematodes and their injurious effects may well antedate history.

The squeamish reader will not enjoy a paragraph which tells of the details and abundance of these parasites in human beings and the lower animals. I have removed from the stomach of a wallaby weighing not over 50 pounds no less than 40,000 nematodes varying in length from a few millimeters to several inches. As for human beings, there are regions where the inhabitants are pot-bellied owing to nematode infestation and where it is not an unheard-of thing for an infested individual to vomit a pint or more of "stomach worms"—parasitic nematodes infesting the human stomach. Such conditions are most prevalent among savages and ignorant people, and it is readily believable that in ancient times the conditions were more favorable to these parasites than they are to-day. Hence, it is easy to understand how a theory of disease based on the prevalence of nematodes could have arisen and gained a wide currency.

In modern times we have come to know much more about such diseases and that parasitic species of nematodes cause many diseases of mankind not formerly recognized. The dreaded "hookworm" is a nematode. So is that scourge of the Tropics, the "guinea worm." Trichina,[1] costing civilized nations hundreds of thousands of dollars yearly for the inspection of pork, is a nematode. If raw or insufficiently cooked trichina-infested pork be eaten by human beings, the result is a serious, oftentimes fatal, sickness called trichinosis, epidemics of which have claimed victims by the hundred. Nematodes have recently been suspected, with good show of of reason, of being carriers of cancer. So the list of more or less serious human nematode diseases and ailments might be increased until practically half a hundred had been enumerated.

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[1] Trichinella spiralis.

No less serious are the nematode diseases of plants and of the lower animals. The common gallworm has been found infesting the roots of several hundred different species of plants, among them most of our cultivated crops, and causes an annual loss amounting to millions of dollars. There is another nematode that has at times completely checked the growing of sugar beets in certain regions. The list of serious diseases of this character could easily be increased to dozens. The same is true of animals. Every domestic species, and doubtless every wild, has a number of specific nematode parasites sapping its vitality.

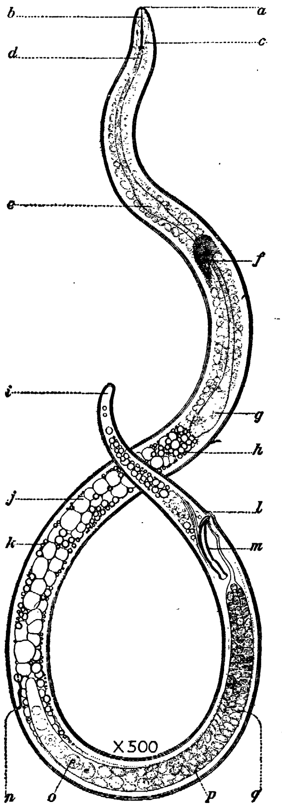


FIG. 33.—One of the injurious parasitic nematodes found in and on the roots of citrus trees, *Tylenchulus semipenetrans*. This is a male. It is the females of this species that are most injurious to the citrus roots. This parasite has been spread throughout the world on the roots of citrus nursery stock. Its original habitat is probably southeastern Asia, whence came our cultivated species of citrus. The females are much larger and penetrate for half their length into the citrus rootlets, leaving the posterior saccate part, devoted to the production of eggs, outside the roots. A new generation is produced every few weeks. These nematodes are devoured by another nematode shown in figure 20, a beneficial species, which hunts and devours this citrus parasite. This is a lateral view of a full-grown male. The spear is usually very inconspicuous—always deteriorated. Note also the deteriorated median bulb, sometimes apparently absent. In the male, in contrast with the female, the anus develops. *a*, Lip region; *b*, spear; *c*, 3-bulbed base of spear; *d*, esophageal lumen; *e*, median esophageal bulb; *f*, nerve ring; *g*, cardiac esophageal bulb; *h*, beginning of the intestine; *i*, terminus; *j*, large intestinal granule; *k*, small intestinal granule; *l*, anus; *m*, spicula; *n*, excretory pore; *o*, spermatocyte; *p*, vas deferens; *q*, spermatozoon.

THE VAST NUMBER OF UNKNOWN SPECIES.

The number of nematode species in existence must be enormously greater than is commonly supposed. Since most species of vertebrates are infested by one or more species of nematode, and with relatively few exceptions a given parasitic nematode infests but one host, it may be estimated that more than 80,000 nematode species infest the forty-odd thousand species of vertebrates. Insects, much infested, will add many thousands of other species. The mollusks, crustaceans, and various groups of worms are also infested, and investigation continues from these sources also to augment the number of known species of parasitic nematodes.

Numerous as the parasitic species are, it is certain that the species of nematodes living free in soil and in water far outnumber them; and the number of free-living individuals is

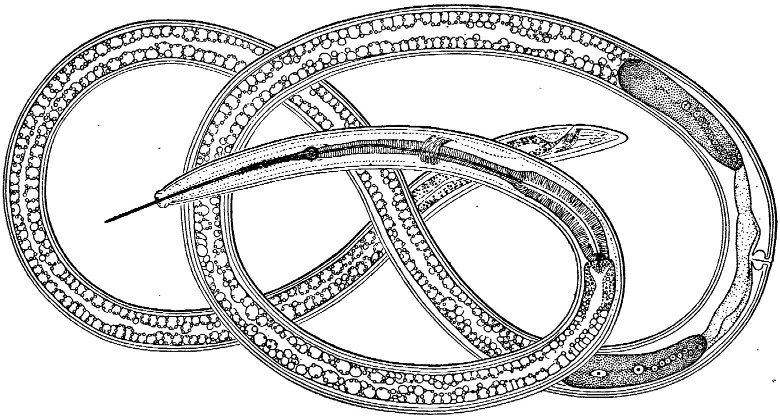


FIG. 34.—This little serpentine monster, the dagger nematode (Xiphinema) is able to coil itself about the rootlets of plants in such a way as to use efficiently its very long and slender spear, which can be thrust far into the root tissues. The spear is clearly to be seen; its more slender anterior part is exserted. This species is found in all parts of the United States and is a representative of an injurious genus, found in many parts of the world. It is able to pierce tougher and more corky roots than those nematodes which are armed with less formidable spears.

so great that they probably constitute one of the important mechanical as well as biological factors in soil and in the bottoms of lakes and oceans. Estimates based on the writer's investigations show that in the upper foot of an arable soil the number of nematodes runs to thousands of millions per acre. Aquatic nematode species exist in enormous numbers in both fresh and salt water, while the number of individuals is past computation.

Of course these large figures are the results of estimates, but the estimates are based carefully on past experience, and they are, moreover, being continually justified by investigations now in progress. A short time ago the writer agreed to prepare a nematode chapter for a college text-book devoted to North American fresh-water organisms. On looking up the literature it was found that there was not a single adequately described North American species of fresh-water nematode. There was little time or opportunity to search specially for these fresh-water forms, and yet it has been possible in this short time to discover about a hundred hitherto unknown kinds representing 30 genera. This ready assembling of so many different genera and species is fresh evidence of the enormous abundance and multifarious nature of these organisms. No doubt there is a horde of species awaiting discovery in North American waters.

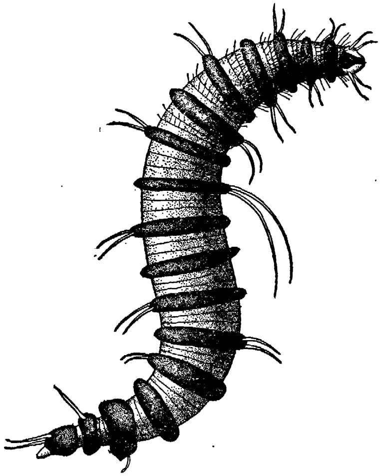


FIG. 35.—The banded nematode, Desmoscolex, one of a rather extensive group, not until 1889 definitely recognized by anyone as nematodes. Their internal organization is concealed beneath a rather opaque cuticle. Their internal anatomy is of a typical nematode character.

Something over a year ago a new genus of nematodes was found attacking citrus roots in California. Within six months this newly discovered citrus parasite was located in such widely scattered regions as California, Florida, Spain, Malta, Palestine, and Australia, showing, incidentally, that the parasite is one that has probably long infested the citrus species and inadvertently has been carried in nursery stock to many different parts of the world from its original habitat, which is most probably the original habitat of the cultivated citrus species themselves—southern Asia. Here again the investigations have disclosed a large number of new species, toward 100 in fact, assembled on and about the roots of citrus trees in various parts of the world.

These are not isolated and exceptional instances, but typical cases. It will be seen, therefore, that it is something more than a mere reconnoissance that leads me to the conclusion that over nine-tenths of the nematode species still remain unknown, a greater disproportion between the known and the unknown than exists in almost any other class of organisms.

There must be hundreds of thousands of species of nematodes. Of this vast number only a very few thousand have been investigated, and of these, comparatively few with any degree of thoroughness.

WONDERFUL VARIETY OF HABITAT.

Not the least interesting thing about nematodes is the astounding variety of their habitats. They occur in arid deserts and at the bottoms of lakes and rivers, in the waters of hot springs and in polar seas where the temperature is constantly below the freezing point of fresh water. They were thawed out alive from Antarctic ice in the far south by members of the Shackleton expedition. They occur at enormous depths in Alpine lakes and in the ocean. As parasites of fishes they traverse the seas; as parasites of birds they float across continents and over high mountain ranges. Their eggs and larvæ, invariably of microscopic size, are carried from place to place by an exceedingly great variety of agencies. Almost any visible thing that moves is capable of transporting nematode eggs or larvæ. Sometimes the eggs and larvæ are so resistant to dryness that long after conversion to dust they may revive when moistened. This revival of "mummified" nematodes may take place after as long a period as a quarter of a century.

Nematodes are found in queer places. The wildest imagination could hardly outpicture the facts. One species is found in the vermiform appendix of man; another has its adult form only in the seeds of wheat. A third form occurs in the felt mats on which the Germans are accustomed to set their mugs of beer, and has thus far been found in no other habitat. On the feet of birds and insects the eggs, larvæ, and adults of certain nematodes are carried to the tops of the tallest trees. The sour sap issuing from the wounds of a tree, often many feet above the ground, not infrequently contains nematodes that are specific to the wounds of that particular kind of tree. The tap water of even well-conducted cities often contains nematodes, for nematodes are common in the potable water of our lakes and rivers.

ABUNDANCE OF NEMATODES.

Nematodes, therefore, are extremely widespread, and to be found in most unexpected places; they are also inconceivably abundant. We little realize the enormous numbers in which these organisms exist all about us, wherever we go, by land or sea. A thimbleful of mud from the bottom of river or ocean may contain hundreds of specimens. The nematodes from a 10-acre field, if arranged single file, would form a procession long enough to reach around the world. A lump of soil no larger than the end of one's thumb may contain hundreds, even thousands of nematodes, and yet present few points that would distinguish it from a lump of soil destitute of these organisms. As nematodes are usually very prolific, a single female ofttimes producing thousands of eggs, the number of eggs vastly exceeds that of the adults.

In short, if all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes, and oceans represented by a film of nematodes. The location of towns would be decipherable, since for every massing of human beings there would be a corresponding massing of certain nematodes. Trees would still stand in ghostly rows representing our streets and highways. The location of the various plants and animals would still be decipherable, and, had we sufficient knowledge, in many cases even their species could be determined by an examination of their erstwhile nematode parasites.

We must therefore conceive of nematodes and their eggs as almost omnipresent, as being carried by the wind and by flying birds and running animals; as floating from place to place in nearly all the waters of the earth; and as shipped from point to point throughout the civilized world in vehicles of traffic.

It is interesting to speculate on what would happen if any great group of plants or animals were utterly destroyed, and such a speculation may serve to throw light on the relative or economic importance of the group. We find microscopic plants living in the sea deriving their sustenance from material they find dissolved in the sea water. These microscopic plants become the food of microscopic animals. The microscopic animals become the food of others of larger size, and so the series continues until it culminates in the great monsters of the deep. These in turn when they die may become dissolved in the sea water, and the material that constituted their bodies may again be taken up by the microscopic plants.

Tiny diatomaceous plants derive their sustenance from sea water, nematodes feed upon the diatoms, fishes upon the nematodes. What would happen if any link in such a chain were destroyed? It is quite conceivable that the destruction of the nematodes might partially depopulate the ocean. Could something of this sort possibly happen in the soil if its nematode millions were suddenly destroyed? It is conceivable, but we do not know.

PREVALENT ERRORS WITH REGARD TO NEMATODES.

The prevalent conception of the nematode organization, even that prevalent among scientific men, is full of errors. These errors glare at us even from the pages of practically all our most modern textbooks and encyclopedias. These misconceptions have arisen in a natural way, because our attention has been largely focused upon the parasitic nematodes. These parasitic species are simple in their external structure, and while vastly larger in body than most of the free-living species, are yet so small that the difficulties of dissection are great if not insuperable. Accordingly, studies have been carried on largely with the aid of thin slices made with the microtome, a method both tedious and difficult. Progress has therefore been relatively slow, so that our knowledge even of these deteriorated parasitic species is often unsatisfactory.

It is a general law that parasitic species become more or less degenerate. Depending as they do upon their host for food and other things, they tend to lose the various organs that would be necessary to them if they led a more active existence. Thus it is that we have parasitic insect forms so degenerate that they possess neither wings nor legs. Their eyes are rudimentary, as are also their antennæ and mouth parts. They are reduced to comparatively motionless worm-like or saccate nearly colorless structures with few of the appendages that form so conspicuous a part of the anatomy of an ordinary insect.

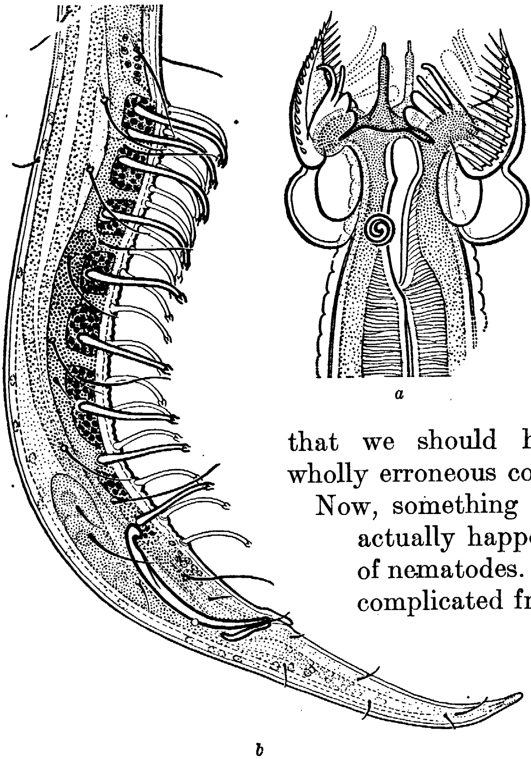


FIG. 36.—Head (*a*) and tail end (*b*) of two different nematodes, illustrating the complicated anatomy of free-living species. Compare these with the relatively simple parasitic forms shown in figure 37. It is by a study of free-living forms that we shall finally arrive at a just conception of nematode morphology.

What would be our conception of the insect group as a whole if our knowledge was largely confined to these simple and degenerate parasitic forms? It is easy to see that we should have derived a wholly erroneous conception.

Now, something of this sort has actually happened in the case of nematodes. While the more complicated free-living species outnumber the parasitic species ten to one, our knowledge of them has lagged far behind that of the parasites, partly because they are minute and hidden away in unexplored locations, and partly because of certain difficulties due to such a peculiarly impenetrable cuticle that it is very difficult to prepare satisfactory material for technical examination.

We have seen that the nematode organism is comparatively complex; at the same time it is almost impossible to determine the function of some of the organs because of our inability to make observations under natural conditions. The problem of studying nematode habits and functions is in some respects similar to that which confronts the geologist in his attempts to form mental pictures of organic activities which took place in remote ages. The geologist must study the relationship of more or less fragmentary elements in a dead condition, and imagine what would happen if these fragments were endowed with life similar to that which comes within our experience in the world as at present constituted. It is somewhat the same with the nematode anatomy. We have before us for study a structure, sometimes living, but more often dead, whose functions we have to surmise on the basis of analogous structures which we may fairly assume to act in accordance with methods to which we are accustomed in a general way, in living organisms of another character and belonging to another group.

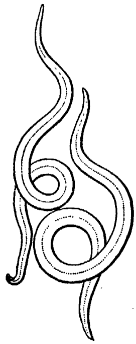


FIG. 37.—Two parasitic nematodes, a male and a female. These are typical parasitic nematodes and represent the ordinary conception of what a nematode is like. We have been misled with regard to nematodes; they are by no means so simple in form as a consideration of the parasitic species would lead us to believe. Compare this illustration with figure 36 which represents free-living nematode forms. The complicated free-living forms more nearly represent the typical nematode structure.

Small wonder then that such conceptions as we have should often prove grossly incorrect. The prevalent idea of the external appearance of a nematode, even among scientists, it is safe to say, approximates to that illustrated in figure 37. As a matter of fact, however, the illustrations on the opposite page are quite as near the truth.

WHAT NEMATODES ARE LIKE; HOW TO FIND AND RECOGNIZE FREE-LIVING NEMATODES.

In answer to the question "What are nematodes like," we can only reply that they do not closely resemble any other organisms. While they constitute a group more widely spread than almost any other, and are numbered by countless millions, their relationship to the rest of the organic world yet remains more or less of a riddle. We may compare the nematodes to an isolated oceanic island whose relation to distant islands and continents remains problematical.

Studying the affinities of insects, for example, it is easy to show that they are more or less closely related to spiders, centipedes, and crabs, and these in their turn to other great groups. Not so with nematodes. There is not another group, great or small, to which they are known to be very closely allied. This isolation in the present organic world is one of the facts that may be used as an argument for the great antiquity of the group. Nevertheless, there is an entire

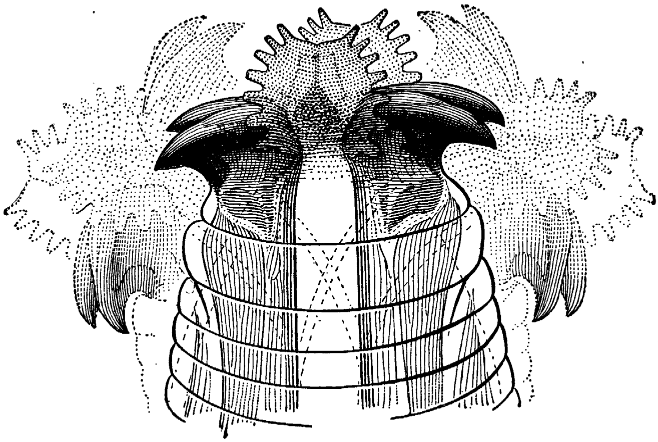


FIG. 38.—Head end of the double-digger, or Diploscapter. This remarkable nematode hooks its way through the soil and tissues of diseased plants by means of a solid piece of armor on the front of its head. With this weapon it can chop both ways, first down and then up. The extreme positions of the digging apparatus are shown by the dotted portions of the figure. With each swing of its head the double-digger hooks its way forward.

absence of evidence that would afford direct proof of great antiquity. No fossil nematodes are known.

HOW TO RECOGNIZE NEMATODES.

Practically any collection of soil, or any collection of sand, mud, or débris from standing or from running water, in any part of the world, will yield, on examination in water with a hand lens, small slender organisms which whip themselves about by means of more or less rapid contortions of the whole body. This type of movement identifies them as nematodes and differs from the movements of other small organisms of similar form in that, though often vigorous and conspicuous, it is in one plane only, the dorso-ventral plane of the body, and in that, unlike worms, the length and proportions of the body meanwhile remain unchanged. In a clear liquid, moreover, this thrashing about seems, as a rule, to produce no locomotion; the nematode remains in about the same spot unless it works its way in among vegetation, débris, or particles of soil. It needs the friction of external matter of this character in order to accomplish its normal locomotion. When quieted by stupefying, or killing, these nematodes are seen to be more or less cylindrical, unsegmented organisms, without locomotor appendages.

COLOR.

An internal examination shows that nearly all the tissues of nematodes are comparatively colorless and transparent, and whatever decided color the body possesses is usually confined to the intestinal region. The cells of the intestine itself are sometimes colored by the presence in them of organic granules of a yellowish, greenish, or brownish tint, and the middle portion of the body is thus made to appear yellowish, greenish, or brownish. The color of the ingested food, showing through the tissues of the body, is also sometimes a color factor; and as the food varies in color from nearly black to colorless, so the nematode is correspondingly tinted. Species feeding on the juices of plants are usually nearly colorless, e. g., species of Tylenchus and Aphelenchus. A considerable number of species possess colored eye spots near the head. In some species the œsophagus contains yellowish or brownish pigment.

HOW NEMATODES WORK.

In answer to the questions How is it that nematodes do so much harm? What are their methods? How do they work? it may be said they bite, puncture, gnaw, suck, and dig as do insects, for instance, but they do all these things with organs of an entirely different character.

The mechanisms with which they accomplish some of these results are very interesting and the study of them constitutes an important branch of nematology. Some of the forms are shown in figures 38, 39, 40, etc. When a nematode is possessed of definite jaws, these are usually three in number, instead of two, as in most other animal groups, and act radially somewhat as do the jaws of a lathe chuck. The jaws are moved by relatively powerful muscles and often are armed with ferocious looking teeth, which can be used in a very effective way. (Figs. 42 and 44.)

Sometimes the mouth is armed with a sting or spear with which to puncture the tissues of the victim, preparatory to sucking away its vital fluids. In such cases, behind the spear and constituting a portion of the gullet, there is a relatively

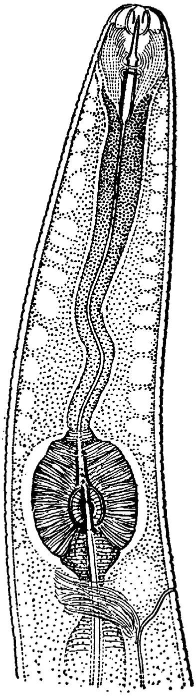


FIG. 39.—Head end of a spear-bearing nematode, showing how the spear mechanism works. The spear is shown with its acute point located in the midst of the lips, and appears in the illustration to be about one-fourth of an inch long. The spear is a hollow tube, and is connected with a very narrow chitinous duct which passes back through the esophagus and connects with the sucking bulb, which is in reality a kind of force pump. This ellipsoidal sucking bulb is shown near the bottom of the figure. The radiating lines shown in the bulb represent muscular fibers. When these fibers contract they open the central valve of the bulb and thus create a vacuum cavity; this in turn creates suction, which extends forward through the narrow tube just mentioned, and so on to the spear, and hence to the lips. If the lips are placed against a moist surface, such as the rootlet of a plant, and the suction pump be then brought into action, the lips become fastened to the moist surface by suction. The lips being now firmly attached, the spear can be brought into play by the contraction of the muscles attached to its base. These are shown surrounding the spear, and are attached to the base of the spear at one end and extend obliquely forward to the base of the lips, where they have their anterior attachment. The contraction of these relatively powerful muscles drives the spear forward and thrusts its point into the tissues fastened against the lips. The suction of the bulb next causes the fluid contents of the cells pierced by the spear to flow through the spear into the esophagus and thence into the pump, which, being a force pump, forces it on into the intestine not shown in the figure.

powerful pump or sucking bulb. The nematode applies its lips to the object to be punctured, exerts suction by means of its muscular pump, thus attaching its lips firmly, and then thrusts its spear through the mouth opening so as to puncture or batter down the tissue containing its food, or through which it wishes to pass. (Fig. 39.)

There is a series of remarkable species inhabiting the soils of our meadows and swamps which possess a powerful spear but no pump. They have developed another and very efficient method of using their spears. These little Iotas, as I have called them, are covered with projecting, retrorse scales, or prickles, so that it is with difficulty that they move in any other direction than forward. Every movement of their bodies drives them in a more or less forthright way through the soil. Coming against the root of a plant, their muscular movements push the head firmly against the surface of the root,

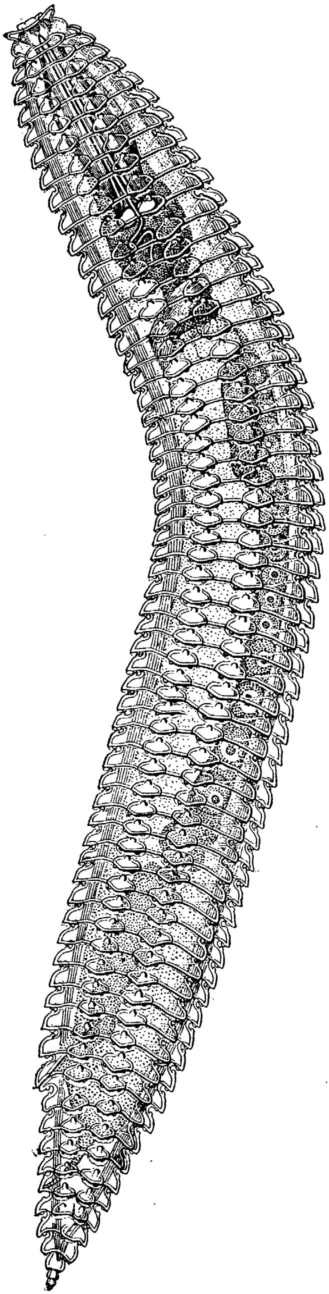


FIG. 40.—One of the scaly little monsters frequenting the soils of our meadows and swamps. These are known as Iotas. They are covered with retrorse scales, or bristles, so that it is practically impossible for them to move in any other direction than forward. Near the head the remarkably large and powerful spear can be seen through the skin. When, in order to make punctures, this spear is thrust out, the nematode is not pushed backward, because of the friction which its scales offer to surrounding soil particles. There are many kinds of Iotas, and all of them appear to be injurious.

so that the spear when thrust forth acts from a well-supported base, namely, the friction of the surface of the body against the surrounding soil material.

Sometimes the secretions or excretions of nematodes are irritating or poisonous, so that their presence in the tissues of animals or plants causes abnormal swellings, or galls. Their presence in the tissues of animals may cause anemia and lassitude, or muscular pains and fever, to say nothing of special swellings, abscesses, punctured blood vessels, paralysis, and insanity.

RELATIONSHIP TO FERTILITY AND BIOLOGY OF THE SOIL.

Notwithstanding the enormous number of nematodes existing in every acre of arable soil, the actual volume and weight of the material composing the nematodes is relatively small. We can not yet positively assert that they assist materially in the fertilization of the soil; it is, however, easily conceivable, in fact, there is a certain amount of evidence for the idea, that, indirectly, some species may be of considerable importance in maintaining or assisting to maintain a fertile condition. Unfortunately, however, we are here driven to speculate on data that are anything but full and satisfactory.

We must have some general notion, not only of the extent of the nematode population of the soil, but also of its composition, before we shall be in a position to do more than reason in a vague and unsatisfactory way upon this subject. We need hundreds of investigators where now there are none, and if these investigators should devote their time for years to come to this subject alone it would only be after a considerable lapse of time that our knowledge of these nematode legions would be sufficient to enable us to reach reliable general conclusions.

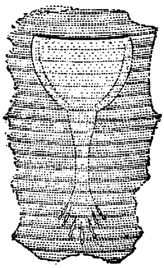
Since the great majority of the nematodes inhabiting the soil are armed with an oral spear, whose sole function, as far as we know, is to puncture other organisms, either animals or plants, presumably plants, we may be strongly convinced that they are on the whole injurious to the roots of the higher plants. In specific cases we have positive proof that this general belief is entirely correct. There are species of spear-bearing nematodes which, by their injurious effects on the roots of plants, cause an annual loss amounting to millions of dollars. It is quite reasonable to suppose that the nematode punctures, even when themselves not a serious setback to the plant that is attacked, nevertheless form a highway for the entrance of other organisms, such as injurious microbes and fungi. In some such way we may account for the enormous mortality of roots. It is an interesting fact that crop plants in what we call good condition are found ofttimes to have a large fraction of their roots in a decayed and useless state. In such cases, where a root is destroyed, often the plant throws out another root higher up on the same axis, and in this way continues to derive its nourishment from the soil. If the plant were freed from the necessity of constantly supplying new roots in place of those killed off, to what extent would this release affect the aerial part of the plant?

Cases are on record, and they are increasing in number, in which it has been observed that if the soil be thoroughly sterlized, and therefore freed, among other things, of its nematode population, and be afterwards inoculated with those microorganisms which are known to be necessary to the health of growing plants, plants reared in it flourish remarkably. May not this luxuriance be due to freedom from injurious underground conditions, prominent among which, we may easily imagine, are the attacks of certain nematodes?

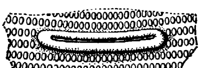
Though nematodes are small they are scattered through the soil in countless myriads in such a way that they must constitute an important mechanical factor. From the time they are hatched until death ensues nematodes seem to be in constant motion. There is no evidence that they sleep, and they rarely remain stationary for more than a few seconds at a time, at least under the conditions in which they come to our notice. Such active organisms, existing as they do in every acre of arable soil in thousands of millions, must exert a more or less powerful mechanical influence.

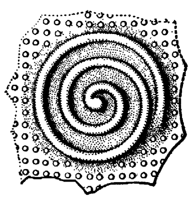
MYSTERIOUS ORGANS—THE AMPHIDS.

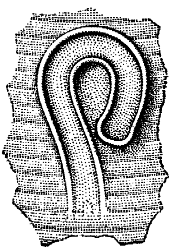
Attention has already been called to the fact that nematodes possess organs the use of which we have been unable to guess. The organs which I have called amphids, occurring as rights and lefts like ears, one on either side of the head, are almost universally present in free-living nematodes. These amphids vary remarkably in size and form (fig. 16), but not much in position. Their regular occurrence in such a prominent location makes it exceedingly probable that they serve some important purpose, but what that purpose is we have not yet discovered. It is suggested by one that they are organs of hearing, and by another that they are breathing organs. It is quite conceivable that they are organs of orientation; that is, organs by which the animal knows what its position is with reference to the action of gravitation—knows when it is right side up. Such organs of orientation occur in higher animals, and are absolutely essential to their well being.

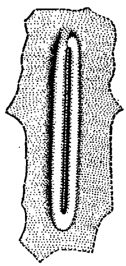


It is possible that the amphids have to do with sensations or functions of which we can form no clear idea. Mark the difficulties that accompany the investigation of such a matter. How are we to interpret the actions of a nematode when trying to determine its sensations and motives, especially if, as is not at all impossible, it is capable of sensations so different from our own that we can not even conceive of them? We have no trouble in proving that a dog hears with his ears as we do. Dissection shows the structure of his ears to be closely like that of our own. We observe how he reacts to various sounds—how he pricks up his ears at a familiar call, or how he fails to hear when his ears are in an unhealthy state. In these observations we are guided by the dog's actions, which we interpret in accordance with our knowledge of our own feelings and actions under similar circumstances. But how can we prove that a nematode hears? How will it act if it does hear?









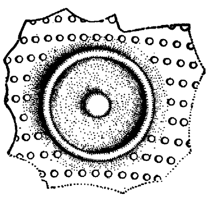


FIG. 41.—Six different forms of the peculiar organs called amphids, almost universally present on the heads of the free-living nematodes. These organs are one of the mysteries of nematology. Nobody knows what they are for. They occur like ears, one on each side near the head end. Sometimes they are of relatively large size.

It is true we can show after a fashion that nematodes, or at least some of them, feel, see, taste, and smell, though in these last two cases there is some doubt as to particulars; that is to say, they act under appropriate circumstances as we imagine they would act if they could feel, see, taste, and smell somewhat after the human fashion. Moreover, we have located and studied the organs through which these sensations may probably be received. But no one has proved that nematodes hear.

As might be surmised from the fact that nematodes live under such a great variety of conditions, their food is extremely varied. Among the parasites, some feed upon living blood, others upon various animal serums and secretions. The plant parasites feed upon the sap and protoplasm found in the tissues of the host plants. The free-living sorts sometimes feed upon small organisms of various kinds—microbes, algæ, the mycelium and spores of fungi, etc., each species having its own particular preferences. Few are omnivorous. Some species found in mud and slime extract food and nutriment therefrom, somewhat as earthworms do, by swallowing material indiscriminately.

NEMATODES IN TREES; HOW DO THEY GET THERE?

The nematode population of trees is worthy of account. It is not generally known, in fact it is practically unknown, that nematodes are found in trees, even to their very tops. Their microscopic eggs and larvæ are carried thither by currents of air, by insects, by birds, and by climbing animals; or, keeping pace with the growth of the tree, the nematodes may reach these high locations by their own efforts. Each kind of tree may have its own peculiar fauna. It is well known that nematodes are the cause of swellings or galls on the aerial parts of plants as well as on their roots. These galls have been a subject of interest for a long time, and have been described and figured in scientific and horticultural publications for half a century or more, but it is only recently that we have come to understand how extensive is the nematode tree population apart from the producers of galls. The crevices in the bark, the natural clefts in the axils of branches and leaves, all furnish suitable lodgment for nematodes, and the nematodes are there, no doubt often harmless, beyond doubt also sometimes detrimental. A few examples may be cited to illustrate this fact.

Not long ago I had occasion to examine some diseased apples which grew high up on an old apple tree, some 20 to 30 feet from the ground. I found the apples infested by nematodes. By experiment I proved that wasps and other insects carried the eggs and larvæ of the nematodes from apple to apple on the tree, and from apples on the ground to others on the tree. The intensity of the infestation may be judged from the fact that a single apple contained nematodes to the number of about 90,000. These were of several different species, some of which were well adapted for forcing their way unaided into the apples, that is to say, were armed with mouth parts specially adapted to puncturing and battering down vegetable tissue. Others belonged to genera characterized by the secretion or excretion of material which appears to aid in dissolving vegetable tissues.

FIG. 42.—Front view of a nematode monster which feeds upon others of its kind. The drawing of the head is correct in every particular. The body has been sketched by the artist to assist the imagination in picturing how one of these organisms looks when seen from in front. The artist's conception is undoubtedly very nearly correct. It will be seen that this little monster possesses three jaws, as do most nematodes. This gives to the mouth opening and pharynx of these organisms a peculiar three-angled or three-sided appearance. The jaws are nearly always of practically equal size, although one of them is morphologically equivalent to the other two.

On another occasion, an examination of the "sap" issuing from a wound in a chestnut tree, high above the ground, showed that this liquid or semiliquid substance was swarming with nematodes.

Finally, an examination of galls of unknown origin on a chestnut oak showed them to be regularly inhabited by no less than four different species of nematodes, some of which were of so peculiar a character as to strongly suggest that these galls are their normal habitat.

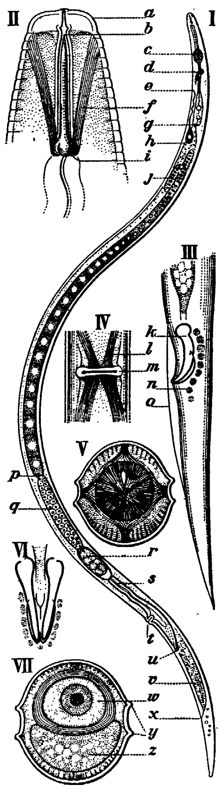


FIG. 43.—The devastating nematode of the onion and other bulbous crops (*Tylenchus devastatrix*). This nematode has caused enormous damage in the Netherlands and other parts of Europe, where it attacks the onion, hyacinth, and numerous other plants. It has been known for a long time in Europe and Australia; no means have yet been devised by which it can be eradicated. Recently it has been found also in the United States. It is one of the species which puncture the tissues of plants by means of a long, narrow, tubular sting, or spear, located in the mouth. *I*, A female; *II*, head of the same more highly magnified, the spear is most clearly shown; *III*, tail of a male; *IV*, vulva from below; *V*, cross section of the neck passing through the sucking bulb; *VI*, front view of the spicula and accessory parts; *VII*, cross section through the middle of a female, showing how the body cavity is filled completely by the ovary (*w*) and the intestine (*z*). *a*. Lip region; *b*, tip of spear; *c*, medium sucking bulb; *d*, nerve ring; *e*, excretory pore; *f*, muscles for protruding the spear; *g*, posterior esophageal swelling; *h*, excretory gland; *i*, hind end of spear; *j*, loop in ovary; *k*, spiculum, or penis; *l*, muscles for opening the vulva; *m*, the vulva; *n*, glandular (?) bodies; *o*, bursa; *p*, hind end of ovary; *q*, uterus containing spermatozoa and a segmenting egg (at *r*); *r*, segmenting egg; *s*, vagina; *t*, the vulva or female sexual opening; *u*, blind end of posterior rudimentary ovary; *v*, intestine, showing its cellular structure; *w*, cross section of an egg; *x*, anus; *y*, wings of the cuticle; *z*, cross section of the intestine.

Such cases, selected more or less at random from those under investigation, are entirely typical and show conclusively that our cultivated and forest trees from their roots to their tops furnish lodgement and food for nematodes peculiar to the situation.

EGGS ALWAYS MICROSCOPIC.

A most striking and important matter connected with the life history of nematodes is the fact that the eggs are always microscopic. There are nematodes which reach a length of several feet, yet their generative cells are always exceedingly minute, comparable indeed with the spores of fungi, or even with the larger microbes. This fact, together with the enormous number of the eggs, is one of the most important things to remember in connection with sanitary measures directed toward diseases caused by these organisms. We have to remember that they do not necessarily indicate their presence by anything that we can see. One contracts hookworm disease as one contracts typhoid, through an invisible agency composed of microscopic elements capable of causing the disease. A field of beets, onions, or potatoes becomes infested, it may be, from invisible eggs or larvæ planted with the seed. The eggs or larvæ of nematodes may be transferred in all the numberless ways rendered possible by their microscopic size.

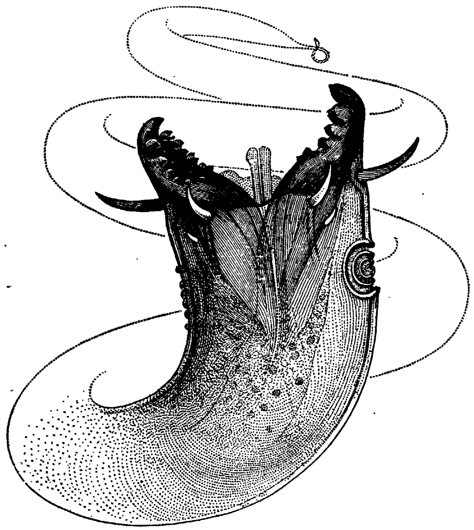


FIG. 44.—The shark nematode, Selachinema. This rapacious little monster preys on other nematodes. The specimen from which the illustration was derived may have had an accident, as one of the jaws, that on the far side, appears to be missing. This nematode has been called the shark nematode on account of the rows of ferocious-looking, backward-pointing teeth with which its jaws are armed.

The difference between the size of the parent and its offspring is often very great. There is a little nematode common in our brooks and ponds that has a total length of about a millimeter. These little specks are the source of another generation in which each individual is a thousandfold larger than either of its parents.

LENGTH OF LIFE.

How long does a nematode live? Easy to ask, difficult to answer. How long does a vertebrate live? It depends on the vertebrate, whether it be a mouse or an elephant. The nematodes constitute a group probably ten times more numerous in species than the vertebrates, and are correspondingly varied in their size, habits, and life history, and, naturally enough, vary also in the age to which they live. It is certain that the eggs and larvæ of some species of nematodes will remain alive under suitable conditions for a very long time. The larvæ of certain nematode parasites have been known to remain alive in a dry condition for approximately a quarter of a century.

Certain forms parasitic in animals require more than one host for their full development. They enter the first host in a larval condition and after certain changes encyst themselves in the tissues of this host and enter upon a period of quiescence, which no doubt may last in some cases for several years, though just how long we do not know. These encysted larval forms will not continue their development until their primary host is devoured by a second host, as a wolf devours a pig, or a bird an insect. On entering the second host the encysted larval forms develop, produce young, and die. Here we have a series of events which normally occupies several years and represents the lifetime of the parasite.

REMARKABLE INSTINCTS.

Certain other nematodes escape from their host in the form of eggs or larvæ and in this condition will remain alive for a considerable length of time, it may be months, it may be years. During all this time they undergo very little change, and yet upon the arrival of suitable conditions they immediately spring into activity. I may illustrate this point by an account of experiments I once made with eggs of the ordinary Oxyuris of man. The eggs of this parasite on leaving the host often contain immature embryos. These embryos will grow slowly in water and other liquid media, but will not rupture the egg shell. I endeavored to assist their escape by cultivation in a great variety of artificial digestive fluids such as pepsin, but all to no purpose; and yet when these eggs were placed in a capsule and swallowed under such conditions that the action of the stomach would cause the capsule to be promptly supplied with fresh normal human digestive fluid at body temperature, the eggs hatched in a

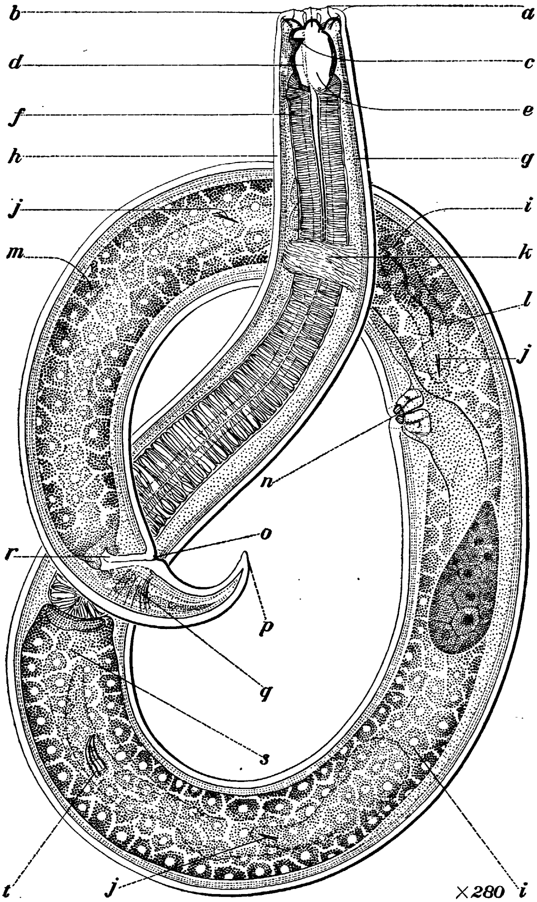


FIG. 45.—This savage little monster is found on or near the roots of plants, where it moves about actively thrusting its head hither and thither with an almost inconceivably rapid motion, hunting other nematodes, which it swallows whole. In the individual illustrated the remains of several victims can be seen through the rather transparent walls of the intestine. This is a beneficial nematode, the *Mononchus papillatus* of Bastian. It has been found feeding upon Tylenchulus, another nematode injurious to the roots of citrus trees. The illustration shows a rather immature femal especimen which has been feeding upon *Tylenchulus semipenetrans*. The remains of three or four Tylenchuli are to be seen in the intestine. *a*, Two of the innervated papillæ existing on one of the six mobile lips; *b*, one of the lips; *c*, dorsal pharyngeal tooth; *d* .one of the three longitudinal chitinous ribs of the pharynx; *e*, pharyngeal cavity; *f*, esophagus; *g*, muscular layer of the body; *h*, cuticle; *i*, one of the cells of the intestine; *j, j, j*, oral spears of three ingested Tylenchuli, the spear in the intestine near the vulva is accompanied by an undigested portion of the lining of the esophagus of the Tylenchulus; *k*, nerve ring; *l*, blind end of the anterior ovary, which, being behind the intestine, shows less clearly than the posterior ovary; *m*, nucleus of one of the intestinal cells; *n*, vulva; *o*, anus; *p*, terminus; *q*, anal muscles; *r*, rectum; *s*, cardia; *t*, spicula of an ingested male Tylenchulus, the outlines of the undigested tail end of which are to be seen faintly.

few hours. So it is with many other nematode parasites. They promptly recognize the specific conditions necessary to their further development, but until those particular conditions are fulfilled they remain quiescent. These quiescent periods, of course, are an element in the age to which the individual lives. Thus it is that while some nematodes mature and die in a very few days, others may live for many years.

Attention has already been called to the fact that nematodes feed upon other organisms. In this way they may be either injurious or beneficial; the net result from an economic standpoint depends on whether the organism devoured is itself harmful or beneficial. There is a nematode that feeds upon the roots of citrus trees and is therefore injurious. (Fig. 33.) Living in the orchards with this first and harmful species is a second nematode that regularly feeds upon the first, and is therefore beneficial, doing the orange grower a good service. (Fig. 45.) Many injurious insects passing a part of their life in the soil, such as wireworms and cutworms, are infested with nematode parasites. These parasites in their larval stage inhabit the soil, where they are picked up by succeeding generations of the insect larvæ. In so far as these parasitic nematodes are injurious to the cutworms they are helpful to the farmer.

Some nematodes therefore are beneficial. We do not know much about these beneficial species, but enough to render the prospect alluring. We know that some of them, especially those living in the soil and in water, feed upon baneful microorganisms such as injurious microbes and fungi, and even upon other nematodes. Doubtless the relationships among these various microorganisms of the soil are as varied and intricate as we know them to be among larger organisms.

Of course it does not necessarily follow that because a soil-inhabiting nematode feeds upon injurious microorganisms it is, therefore, necessarily beneficial, for while feeding on the micro-organisms it may be the means of transporting and transplanting them, just as birds and animals feeding upon obnoxious plants may become a means of distributing the seeds. The subject is full of intricacies.

NEMATOLOGY.

The foregoing fragmentary sketch may indicate to the student, as well as to the general reader, the vast number of nematodes that exist, the enormous variety of their forms, and the intricate and important relationships they bear to mankind and the rest of creation. They offer an exceptional field of study; and probably constitute almost the last great organic group worthy of a separate branch of biological science comparable with entomology—nematology.